

# Hydraulic flow resistance of epigeal and hypogean fish of the family Trichomycteridae (Ostariophysi, Siluriformes)

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## Abstract

Critical swimming speeds of four trichomycterid fish species from epigeal and hypogean environments were analyzed and compared: *Trichomycterus itacarambiensis* and *Ituglanis passensis*, both troglobitic from underground rivers; *Trichomycterus brasiliensis*, from epigeal rivers; and *Ituglanis* sp., an undescribed troglomorphic species from an underground stream. Swimming tests were conducted with a non-volitional apparatus in which fish swim against a progressive incremental water velocity until they longer resist the flow. Total length was significantly related to critical speed for only *T. itacarambiensis*. The critical speed obtained by each species, in decreasing order, with values in lengths per second (lengths/s), were: *I. passensis* (3.61), *T. itacarambiensis* (3.49), *T. brasiliensis* (3.11) and *Ituglanis* sp. (1.89). Swimming performance differed between the congeners *T. itacarambiensis* and *T. brasiliensis*, but did not differed between *I. passensis* and *Ituglanis* sp. The greater speed for the troglobitic species compared to that of the troglomorphic and epigeal species is probably related to seasonal flooding pulses that can be extremely severe in caves. Furthermore, during the tests, fish were observed using their mouth and/or barbels to fasten themselves to the substrate to avoid high flows.



**Keywords**

Caves, critical speed, subterranean rivers, swimming performance, troglobitic fishes

**Introduction**

Fish belonging to the order Siluriformes Cuvier, 1817, usually possess broad geographical distributions, with different species occurring in both freshwater, marine and brackish environments (Froese and Pauly 2019). Among the families of this order that occur in freshwater, Trichomycteridae Bleeker, 1858, stands out as one of the richest, with around 330 species (Fricke et al. 2020) and 42 genera distributed throughout South America, Costa Rica and Panama (de Pinna 1998; Froese and Pauly 2019). Species from this family possess high plasticity in colonizing different environments and are particularly diverse among Neotropical fish (Wosiacki and de Pinna 2008) with representatives in both surface and subterranean waters.

*Trichomycterus* Valenciennes, 1833, is one of the richest genera within the family Trichomycteridae, with more than 240 described species (Wosiacki and de Pinna 2008; Nelson et al. 2016; Froese and Pauly 2019). Species of the genus occur in a variety of habitats, from rocky substrates in small streams with strong currents such as headwaters (Arratia 1983) to extremely diverse habitats such as semi-temporary puddles and streams at high altitudes (Wosiacki and de Pinna 2008).

The genus *Ituglanis* Costa & Bockmann, 1993, also of the family Trichomycteridae, is considered the sister group of *Trichomycterus* (Costa & Bockmann, 1993). Species of the former are distributed throughout South America in epigean and hypogean watercourses (Trajano et al. 2010). There are at least 11 troglobitic species of the family Trichomycteridae in Brazil, three of which belong to the genus *Trichomycterus*, including an undescribed species (Proudlove 2010; Bichuette and Rizzato 2012), and six to the genus *Ituglanis* (Proudlove, 2010; Rizzato and Bichuette 2014). Furthermore, both *Trichomycterus* and *Ituglanis* contain species with subterranean populations, with many of them possessing troglomorphic traits (e.g. reduction of ocular structures and melanistic pigmentation) (Fernández and Bichuette 2002), and are the two genera that best represent the family Trichomycteridae in hypogean environments (Trajano et al. 2010).

Many catfish species, but especially trichomycterids, are mainly found in basin-level streams and vadose tributaries, sometimes also occurring in subterranean aquatic environments, as previously mentioned. However, subterranean environments present particular hydraulic conditions with fast changes in water flow, which varies sharply according to the intensity and frequency of rainfall (Culver and Pipan 2009; Gabrovšek et al. 2018). According to cave morphological traits and variation in the amount of water that enters these environments, internal water flows can occur under the effects of atmospheric pressure or pressures higher than atmospheric (functioning as a forced duct). Furthermore, changes among these two flow regimes can occur markedly in these environments (Hawes 1939; Culver and Pipan 2009).



Studies of swimming capacity in Neotropical fish species are rare (Santos et al. 2007; Santos et al. 2008, 2012; Castro et al. 2010), and even more scarce for underground species (Sampaio et al. 2012). From an ecological and behavioral perspective, such studies can contribute to a better understanding of the specializations possessed by subterranean species for dealing with the hydraulic conditions of cave environments. Under these conditions, species that have higher swimming capacities or are prone to resist flow would possibly be favored, but these aspects have never been evaluated. In this sense, the objective of this work was to compare the swimming capacity of hypogean and epigean fish species of the family Trichomycteridae by estimating their critical speeds and observing any behaviors that may favor their resistance to flow in subterranean environments.

## Materials and methods

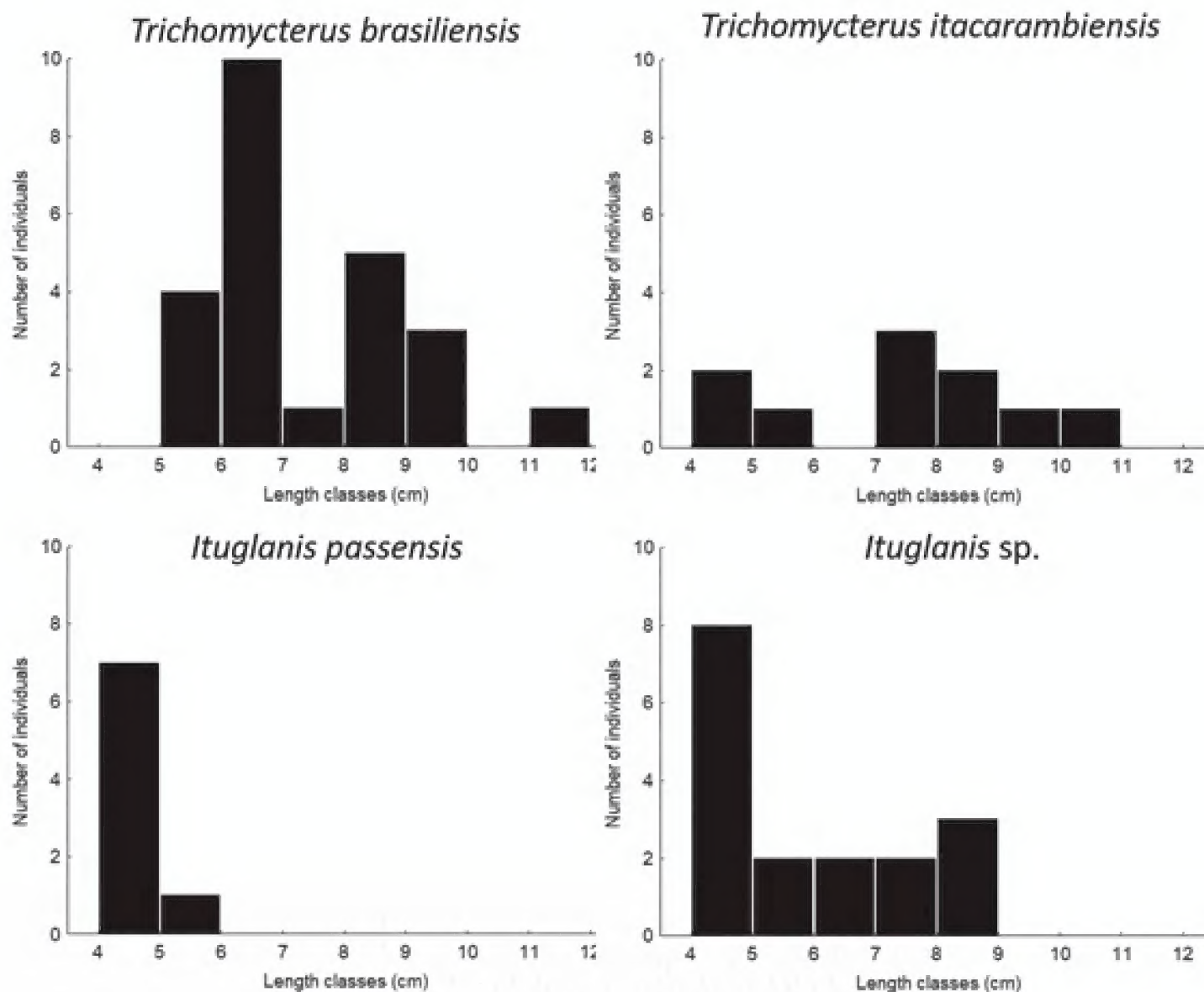
### Studied species, field collection and transportation

Four catfish species of the family Trichomycteridae that occur in Brazil were analyzed: two troglotic, one troglophilic and one epigean. Twenty-four individuals (N=24) of the species *Trichomycterus brasiliensis* Lütken, 1874, which occurs in superficial streams, were caught with a trawl in the city of Luminárias (21°30'52"S, 44°52'29"W), in the state of Minas Gerais (MG). Seventeen individuals (N=17) of the troglophilic species *Ituglanis* sp., which occurs in both superficial and subterranean streams, were collected inside the cave Loca d'Água (20°25'23"S, 45°41'32"W) in the city of Pains, MG. Ten individuals (N=10) of *Trichomycterus itacarambiensis* Trajano & de Pinna, 1996, a troglotic fish which lives only in subterranean environments, were collected in the cave Olhos d'Água (15°07'00"S, 44°10'00"W), in the city of Itacarambi, MG. Ten individuals (N=10) of the troglotic *Ituglanis passensis* Fernández & Bichuette, 2002, were collected inside the cave Passa Três (13°45'00"S, 46°22'00"W), which is located in the São Domingos karst area of the state of Goiás. Cave fish were collected using PVC traps containing chicken liver as bait, from May to July 2008. Authorization for collecting fish was granted by Brazilian Institute of the Environment and Renewable Natural Resources (IBAMA; numbers 13295-1 and 10327-1).

Collected specimens were sedated and transported in a plastic box with aeration for approximately seven hours, after which they were transferred to climate-controlled aquariums at the laboratory. Testing started 48 hours after the arrival of the fish at the laboratory. Adult individuals of different size class were selected and tested in order to analyze fish swimming behavior and critical speed for as wide a size range of fish as possible (Fig. 1).

After testing, the specimens were sedated with eugenol, measured and kept in the aquariums. Individuals that died from natural causes were fixed in formalin and preserved in 70% ethanol. Voucher specimens were properly deposited in the fish collection of Coleção Ictiológica da Universidade Federal de Lavras, Minas Gerais State, Brazil (CIUFLA 0068; 0144; 0145).





**Figure 1.** Number of specimens according to total length (cm) classes.

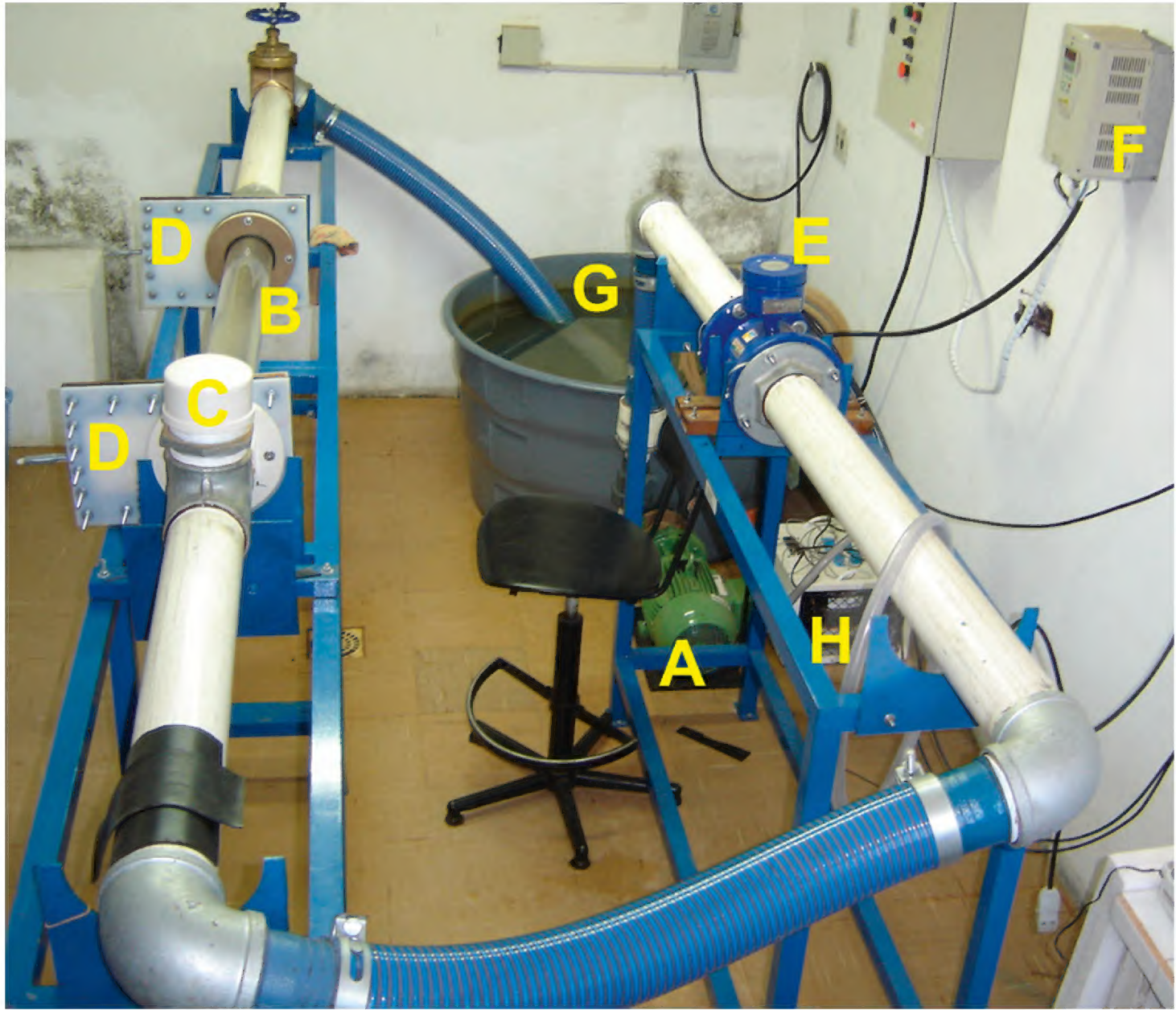
## Apparatus and experimental procedures

The experimental apparatus (Fig. 2) was similar to a Brett respirometer (Brett 1964) and its design followed that proposed by Santos (2007). In the apparatus, the fish specimen swims against water flow created by a centrifugal pump.

During the first 5 minutes (time interval), the mean water velocity in the testing section was maintained at 0.05 m/s and the fish was inserted. The flow velocity was then increased incrementally by 0.05 m/s at a time intervals of 5 minutes. The test finished when the fish experienced complete fatigue, which was assumed with the absence of swimming movements and confinement at the downstream screen. All swimming behaviors were monitored and noted during the tests.

Temperature and dissolved oxygen of the water were monitored once before, during and after the tests (Fig. 2G). Water was maintained at temperatures similar to those of the natural environment where the fish were sampled using a portable cooler (Fig. 2H). We considered a valid test for critical speed to be when the specimen swam for at least 5 minutes (a single time interval), and for swimming behavior when the specimen attached for at least 25 minutes (five time intervals). Specimens that refused to swim or remained attached were not considered in the critical speed analysis.





**Figure 2.** Experimental apparatus for testing fish swimming capacity and resistance to flow: **A** centrifugal pump which creates the water flow **B** central testing section **C** connection for fish entrance to and removal from the central testing section **D** screens to keep fish in the central testing section **E** flow rate gauge **F** frequency converter which was used to change pump rotation and, consequently, the flow velocity in the central testing section **G** water tank and **H** water cooler.

## Data analysis

Absolute critical velocity for each specimen was calculated by the Brett equation (1):

$$V_{crit} = V_{max} + \frac{t_{max}}{\Delta t} \times \Delta U \quad (1)$$

where  $V_{max}$  is the maximum velocity obtained by the fish specimen (m/s),  $t_{max}$  is the maximum swimming time before complete fatigue (s),  $\Delta t$  is the time interval (300 s) and  $\Delta U$  is the velocity increment (0.05 m/s).

After this calculation, the swimming velocity must be corrected ( $V_{corrected}$ ) due to fish obstruction of the effective area for water movement. Equations 2 and 3, which were proposed by Pope and Rae (1966), provide the corrected critical velocity:



$$V_{corrected} = \frac{V_{measured} K_3 \tau_1 (Volume)}{C^{3/2}} \quad (2)$$

$$Volume = 0,45e^2L \quad (3)$$

where  $V_{measured}$  is specimen critical velocity (m/s),  $K_3$  is a coefficient that depends on the ratio between fish width ( $e$  in cm) and fish total length ( $L$  in cm) and may be obtained following Pope and Rae (1966),  $\tau_1$  is a factor which depends on the cross sectional shape (for circular shape we adopted 0.8),  $C$  is the area of the cross section of the central testing section (cm<sup>2</sup>),  $Volume$  is fish volume (cm<sup>3</sup>) and  $e$  is calculated as the average between the maximum width and fish length (cm).

Linear regression provided the relationships between critical speed and other variables for each species: fish total length, fish standard length, water temperature and dissolved oxygen. Factorial Analyses of Variance (ANOVA) compared critical speed among the studied species, for which relative critical speed (body length/s) was utilized (i.e., critical velocity corrected by fish standard length). This speed relativization allows comparisons of swimming speed to be made between different specimens and species and is based on the influence of fish body size on swimming capability. Relative critical speed was also compared for pairs of species of the same genus using the Levene test. The significance level was 0.05 (p-value) for all tests and the statistical analyses were conducted using Statistica 7.0.

## Results

Tests starting with a water velocity of 0.05 m/s and with progressive increments of 0.05 m/s every 5 minutes revealed that at velocities under 0.5 m/s all fish remained active, swimming normally and sometimes remaining still over the acrylic surface (Fig. 2B). With velocities greater than 0.6 m/s, some individuals did not swim, but instead resisted the flow by attaching themselves to the steel screen using their mouths, barbels or even odontoids, and reaching high values of critical speed (Table 1). Some fishes also exhibited short and fast swimming bursts, with strong propulsions against the flow.

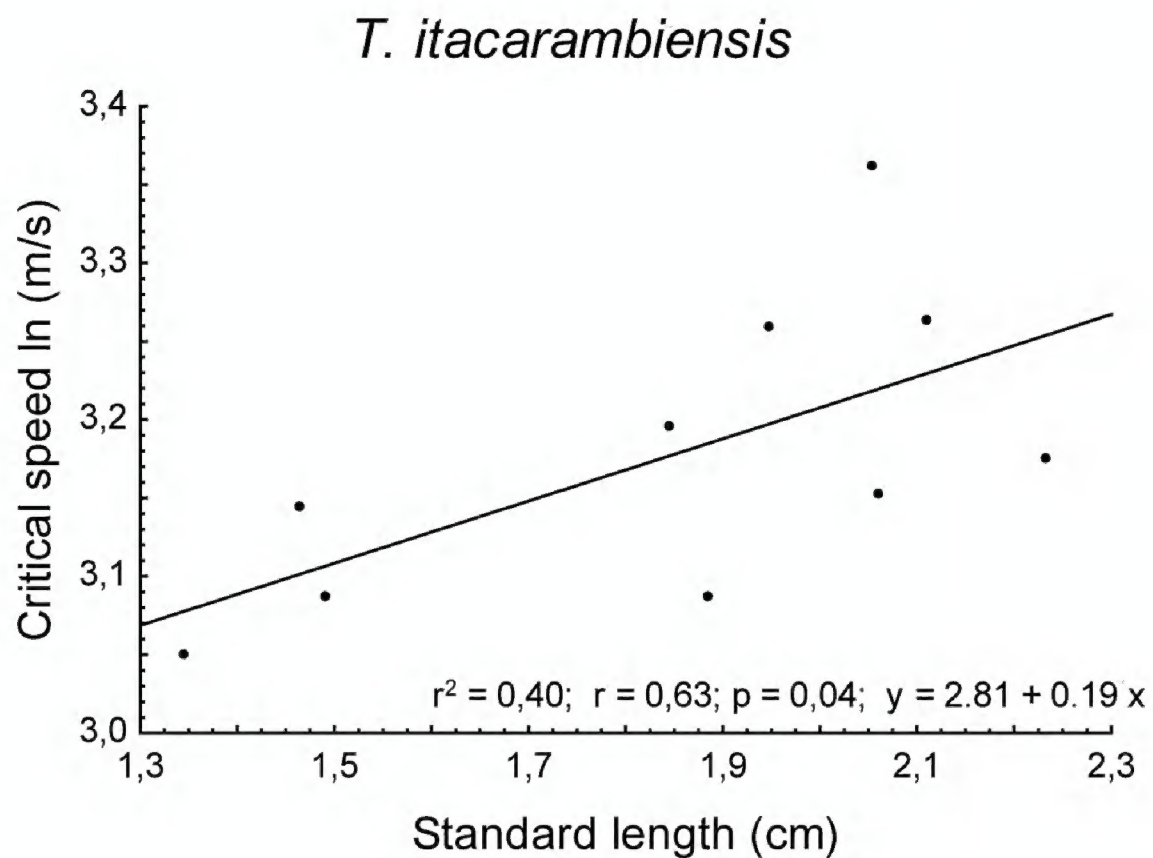
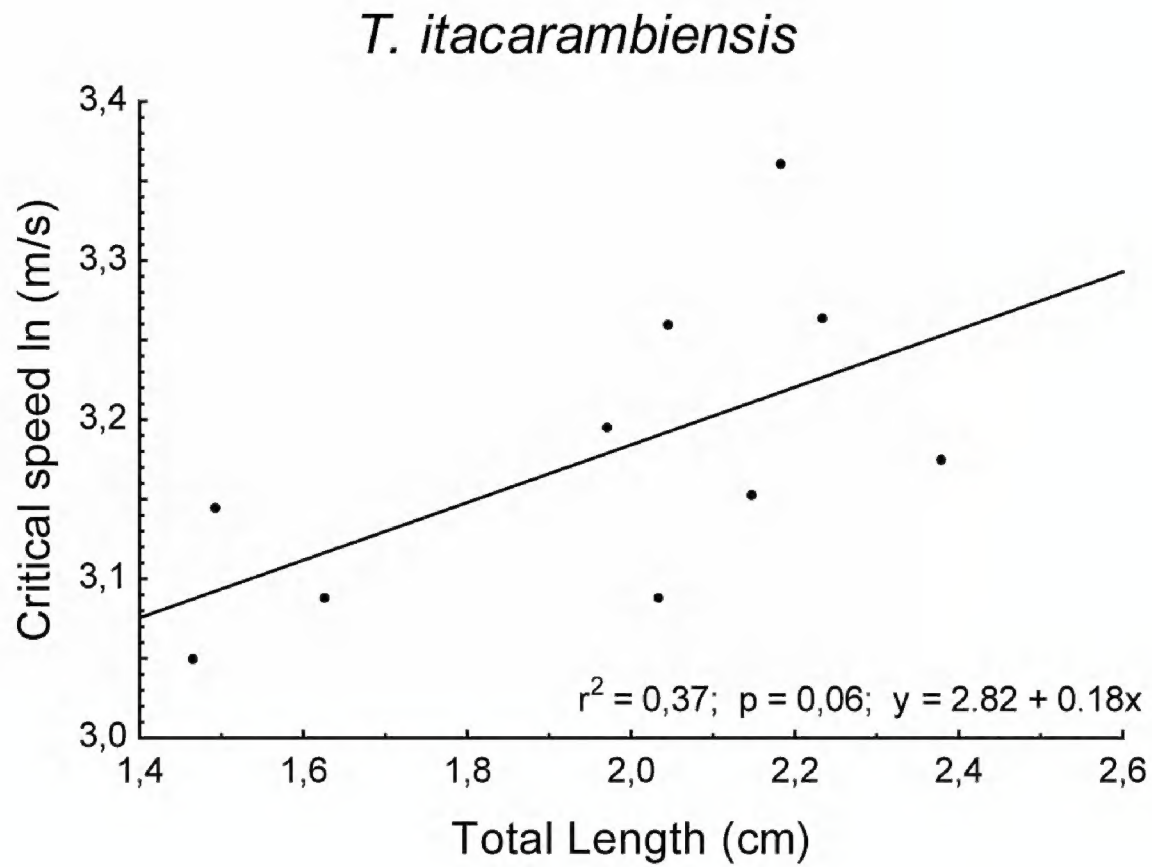
No significant relationships ( $p > 0.05$ ) were observed between critical speed and water temperature and dissolved oxygen for any of the tested species. Only for *T. itacarambiensis* was critical speed related to total and standard lengths, the latter with greater explanatory power (Fig. 3).

Despite not being significantly related to critical speed, temperature and dissolved oxygen values were maintained as close as possible to the respective environments of origin of the fish during the tests (Table 2).

Absolute critical speed differed among the tested species ( $F = 7.72$ ;  $p < 0.01$ ), with *Ituglanis* sp. having the lowest swimming capacity (Table 3).

**Table 1.** Attributes related to attaching behavior of each tested species.

	<i>T. brasiliensis</i>	<i>T. itacarambiensis</i>	<i>Ituglanis</i> sp	<i>I. passensis</i>
Species habit	Epigean	Troglobitic	Troglophilic	Troglobitic
Number of tested individuals	24	10	17	8
Attaching behavior (number of individuals)	3	0	3	2
Maximum water velocity endured by attaching (length/s)	9.94	–	4.62	9.20

**Figure 3.** Relationship between absolute critical speed (ln) and total length and standard length, for *T. itacarambiensis*.



**Table 2.** Temperature and dissolved oxygen values during testing.

Species	Temperature (°C)				Dissolved oxygen (mg/L)			
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
<i>T. itacarambiensis</i>	18.4	18.0	19.3	0.44	8.4	8.2	8.6	0.15
<i>T. brasiliensis</i>	23.2	22.0	24.0	0.97	8.3	8.2	8.6	0.16
<i>I. passensis</i>	19.7	19.0	21.3	0.93	8.2	–	–	–
<i>Ituglanis</i> sp	19.7	18.5	20.6	0.70	8.2	–	–	–

**Table 3.** Relative and absolute critical speeds for the tested species considering specimens that swam in at least one time interval.

Species	Relative Critical Speed (Lenght/s)				Absolute Critical Speed (m/s)			
	Mean	Min.	Max.	SD	Mean	Min.	Max.	SD
<i>T. itacarambiensis</i>	3.496	2.208	5.213	0.980	0.240	0.211	0.288	0.023
<i>T. brasiliensis</i>	3.115	1.872	5.486	0.947	0.228	0.132	0.324	0.045
<i>I. passensis</i>	3.615	2.583	5.532	1.275	0.233	0.176	0.343	0.071
<i>Ituglanis</i> sp	1.896	0.739	3.387	0.838	0.137	0.063	0.236	0.056

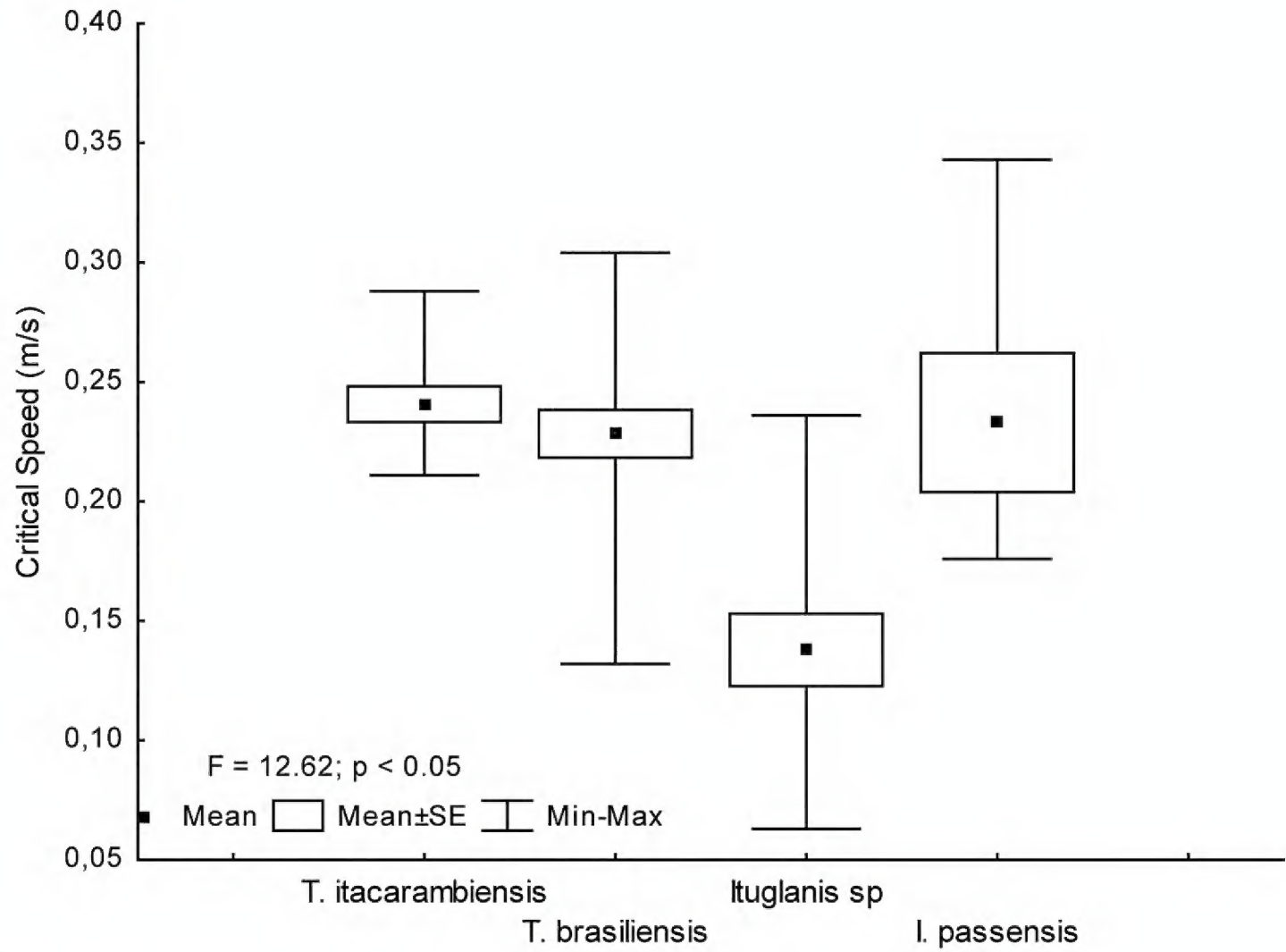
When comparing pairs of congeneric species, *Ituglanis* sp. had lower speeds ( $p < 0.01$ ) and smaller variance in its relative speed ( $F = 2.87$ ;  $p = 0.002$ ) than did *Ituglanis passensis*. For the species of *Trichomycterus*, *T. itacarambiensis* had higher absolute speeds and lower variation ( $F = 4.65$ ;  $p = 0.03$ ) than did *T. brasiliensis* (Figs 4, 5), however, there was no significant difference between their relative speeds ( $p = 0.31$ ).

Discussion

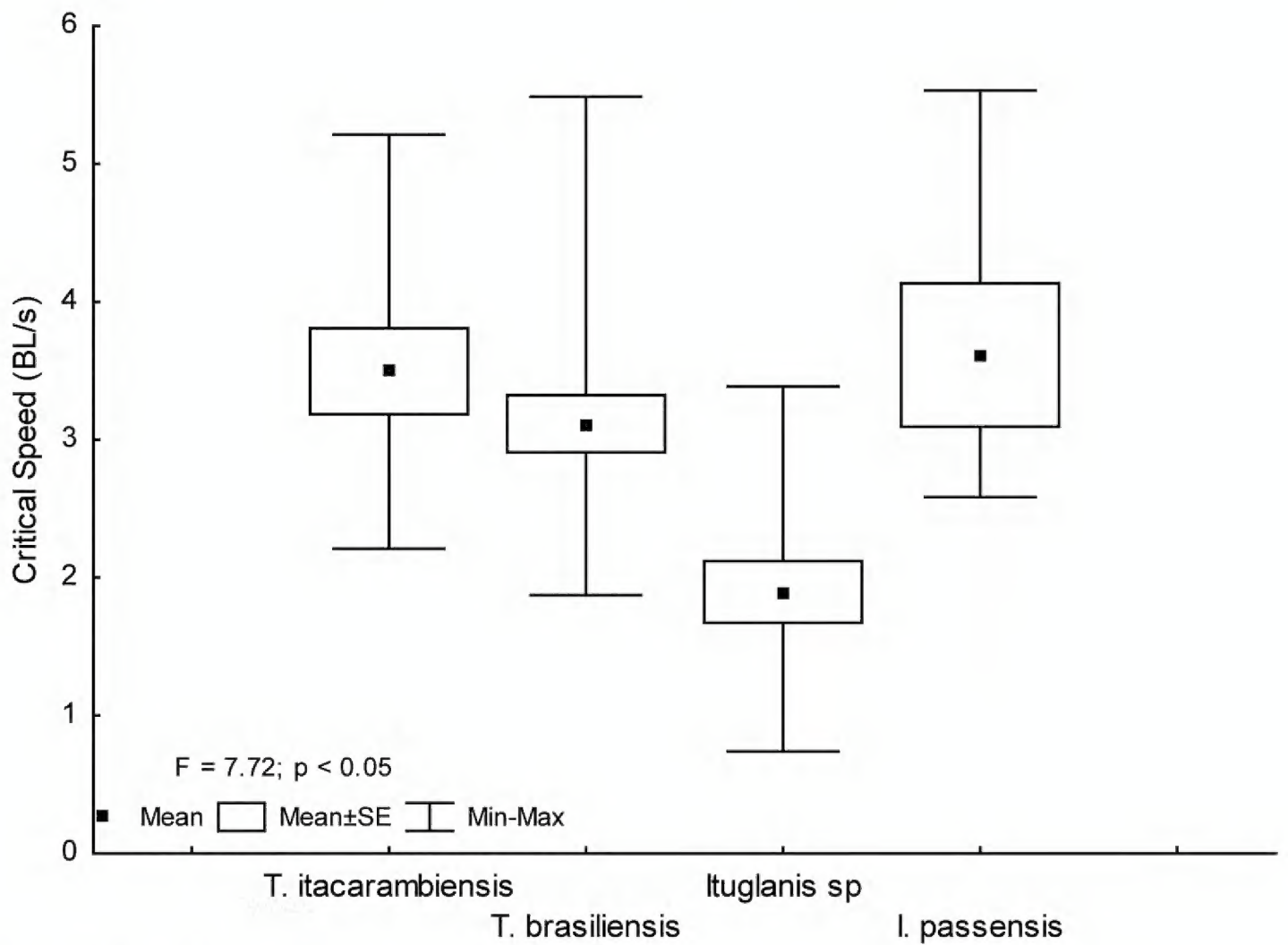
The behavioral capability to resist flow without active swimming, as observed in this experiment for three of the four evaluated species, can be considered an important pre-adaptation to subterranean environments. This ability has already been described for a number of groups of fish, including *Cryptotora thamicola* (Kottelat, 1988), a cave species that can climb waterfalls in its habitat through a distinct type of locomotion and a modified pelvic girdle (Flammang et al. 2016). Other ways to resist flow include the use of pelvic fins (Schoenfuss and Blob 2003) or the mouth (Gerstner 2007) as an adhesion disc, or pectoral fins and their rays (Buckup et al. 2000) or the operculum. In the case of the studied trichomycterids, is related to the ability to remain fixed to the bottom substrate, even during periods of higher flow (Braga 2004).

The ability to adhere to the substrate, as observed for three of the studied species, may represent a pre-adaptation to the cave environment. Some similar behaviors that also support this idea have been verified in troglobitic fish that dig and bury themselves in the substrate (Romero 1987), such as *Trichomycterus conradi* (Eigenmann, 1912), which remains under rocks and between cracks (Brown 1996), as does *Troglichthys rosae* (Eigenmann, 1898), or that hide in the gravel (Schubert et al. 1993), such as *Typhlichthys subterraneus* Girard, 1859. Such behaviors denote flow resistance and even energy savings in these environments.





**Figure 4.** Absolute critical speed (m/s) of the tested epigeal and hypogean species.



**Figure 5.** Relative critical speed (body length/s) of the tested epigeal and hypogean species.



*Trichomycterus itacarambiensis* was the only species that did not resist flow using the mouth or the operculum in the experiments of the present study. Even so, Trajano (1997) observed a similar behavior in a specimen that, despite the fact that it could have been dragged by a strong flood in the underground environment, remained in the same place perhaps due to anchoring with opercular odontoids and hiding behavior. Ecological opportunities and physical challenges of fast-water habitats have dramatically shaped the evolution of freshwater fish all over the world (Lujan and Conway 2015). The capability to resist flow was probably an important mechanism that allowed colonization and persistence by fish in subterranean rivers. This aspect is especially relevant for catfish of the family Trichomycteridae, which inhabit vadose systems where most of the troglobitic species of this family are found (Mattox et al. 2008). In fact, of the 33 troglobitic fish described for the Neotropics (Niemiiller and Soares 2015), 20 belong to the genera *Trichomycterus* and *Ituglanis* (Rizzato & Bichuette, 2014).

*Trichomycterus itacarambiensis* was the only species to show a significant relationship between critical speed and total and standard length. Total length is considered a variable of strong explanatory power for the swimming capacity of fish (Watson and Balon 1984; Wikramanayake 1990), as verified for *Pimelodus maculatus* Lacépède, 1803, and *Megaleporinus reinhardti* (Lütken, 1875), two Neotropical species found in Brazilian rivers (Santos et al. 2007; Santos et al. 2008), and for the troglobitic Brazilian species *Stygichthys typhlops* Brittan & Böhlke, 1965 (Characiformes) (Sampaio et al. 2012). This relationship between speed and length suggests a greater capacity for movement. *Trichomycterus itacarambiensis* is the least sedentary species compared to other cavefish, being capable of undertaking movements over a distance of more than 100 meters in periods of one to five months in a study carried out with recapture of troglobitic fish in Brazil (Trajano 1997, 2001).

On the other hand, the higher speeds observed for the troglobitic species, in comparison to their epigean relatives, may be directly related to selection exercised by the hydraulic cave environment where they live. It is important to note, however, that underground habitats do not always exercise the same type of hydraulic selection. As an example, the troglobitic species *S. typhlops* presented a lower critical swimming speed than the other related epigean species tested, *Piabina argentea* Reinhardt, 1867, *Piabarchus stramineus* (Eigenmann, 1908) and *Hemigrammus marginatus* Ellis, 1911 (Sampaio et al. 2012). This was probably due to the fact that this species is associated with phreatic habitat, which is characterized by the lack of directional flow that would impose strong hydraulic pressures (Sampaio et al. 2012). Differences observed on the speed of troglobitic Siluriformes and Characiformes indicates the great variability of hydraulic habitats that exist underground. The development of a swimming capability sufficient to resist flood pulses throughout the isolation period may have guaranteed catfish survival in subterranean streams and, thus, was incorporated into the populations over time.

In addition to extreme events arising from large flow pulses (Gabrovšek et al. 2018), high water speeds and slightly reduced space availability also characterize subterranean streams (Ford and Williams 2013). Such characteristics can provide environments with less complexity when compared to surface streams (Culver and Pipan 2009). Furthermore, the scarcity of organic substrates commonly found in such environments (Ratton et al. 2018)



contributes to their homogenization, since the presence of such substrates at the surface determines more heterogeneous environments with lower flow rates (Entrekin et al. 2008).

Selection favoring specimens with higher swimming capability would also explain the less variation in this ability observed in cave species. Such a pattern would fit the definition of directional selection, when fitness consistently increases (or decreases) with the value of the characteristic, reducing the variation in a population (Kingsolver and Pfennig 2007). Some similar adaptations observed in cave fish belonging to distinct taxa suggests that adaptation to the subterranean environment may be a process resulting from similar selective pressures (Niemiller and Soares 2015).

In contrast, less variation in the swimming capability of cave species could also be explained by stabilizing selection, in which the average values of a give trait in the population (in this case, swimming capability) have greater aptitudes than the extremes, which are negatively selected (Ridley 2009). In this case, average swimming values would be favored, reducing extremes that could be disadvantageous and costly in an oligotrophic environment, as suggested by Sampaio et al. (2012) to explain the limited intraspecific variation observed in the swimming capacity of *S. typhlops*. It should be noted, however, that part of the differences observed in the present study may be related to the small number of tested troglobitic individuals.

The type of swimming performed by a species has direct implications on its habitat use (Wainwright et al. 2002) and the range of swimming speeds exhibited by the fish species in the present study is consistent with the water speed found in each of their original environments. This indicates a close relationship between this swimming speed and environmental traits (Fulton et al. 2005), suggesting adaptation to the habitat in which the fish occur. The critical swimming speeds observed in the present study contribute to increasing the knowledge of each of the studied species. In addition, they enable a better understanding of the functioning of the hydraulic environment with which the species are associated, especially for cave species whose habitats are not always easily accessible. Some behaviors observed in this study, such as the ability to adhere to the substrate, as well as the higher critical swimming speed of the troglobitic species, must constitute, respectively, pre-adaptation and response to the peculiar hydraulic conditions of the cave environment.

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